Abstract.—We examined 1,469 tarpon, Megalops atlanticus, ranging from 102 to 2,045 mm fork length (FL) collected in South Florida waters from 1988 to 1993. Females had a mean length of 1.677 mm FL (n=322) and were significantly larger than males, which had a mean length of 1,447 mm FL (n=125). Ages of 977 tarpon were estimated from thin-sectioned otoliths (sagittae). Eighteen tarpon were marked with oxytetracycline (OTC) to form a reference point on the otolith and were held in captivity for periods ranging from 13 to 50 months. Examination of OTC-marked otoliths suggested that a single annulus was formed each year. Marginal increments of young of the year and 1-year-old tarpon showed a single annual minimum during April-June. Tarpon are longlived and reach a maximum age of at least 55 years. Growth of the tarpon in our study was rapid until an age of about 12 years and then slowed considerably. Male tarpon (n=141) ranged from 0 to 43 years in age, and female tarpon (n=298) ranged from 0 to 55 years in age. The von Bertalanffy growth equation for females was FL = $1.818(1-e^{(-0.103(Age+1.410))})$  and for males was  $FL = 1,567(1 - e^{(-0.123(Age+1.575))})$ . Estimates of the von Bertalanffy growth parameters  $L_{\omega}$  and K for males and females were significantly different. Predicted lengths of females were greater than those of males for all ages greater than 4 years.

# Age and growth of tarpon, Megalops atlanticus, from South Florida waters\*

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Tarpon, Megalops atlanticus, are large, migratory, elopomorphic fish that frequent coastal and inshore waters of the tropical and subtropical Atlantic Ocean. In the western Atlantic, tarpon regularly occur from Virginia's eastern shore to Central Brazil and throughout the Caribbean Sea and the Gulf of Mexico (Wade, 1962; Hildebrand, 1963; de Menezes and Paiva, 1966; Zale and Merrifield, 1989). In South Florida and parts of Central America, tarpon are the basis of economically important recreational fisheries. In Florida, the fishery is intensely regulated, and anglers are required to purchase a permit before harvesting a fish. Since the establishment of the permit system in 1989, the harvest of tarpon in Florida has declined to less than 100 fish per vear, and the fishery is now mostly catch-and-release. Tarpon occur in a variety of habitats ranging from freshwater lakes and rivers to offshore marine waters, but large tarpon targeted by Florida's fishery are most abundant in estuarine and coastal waters. In Florida, the fishery is seasonal; most tarpon are caught during May—July, although some fish are caught in all months.

Tarpon life history has not been adequately described. Breder (1944) examined gonads of tarpon from Florida waters but did not fully describe either temporal spawning patterns or age and size at sexual maturity. De Menezes and Paiva (1966) macroscopically examined gonads of tarpon from Brazilian waters and reported on temporal spawning patterns and size at sexual maturity. Most information on tarpon reproduction in Florida waters has been inferred from early life history studies (Smith, 1980; Crabtree et al., 1992; Crabtree, 1995). Larval distribution patterns suggest that tarpon in Florida waters spawn offshore from May through August (Smith, 1980; Crab-

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tree et al., 1992; Crabtree, 1995). Smith (1980) estimated the length of the larval phase to be 2-3 months, but little is known about the processes that transport larvae from offshore spawning grounds to inshore juvenile habitat. Metamorphic larvae are typically found inshore in mangrove-lined estuaries but also occur in temperate Spartina marshes (Harrington, 1958 and 1966; Erdman, 1960; Wade, 1962; Mercado and Ciardelli, 1972; Tucker and Hodson, 1976; Chacón et al., 1992). Young-of-the-year (YOY) tarpon occur in small stagnant pools and sloughs of various salinities and have been reported from North Carolina (Hildebrand, 1934), Georgia (Rickards, 1968), Florida (Wade, 1962 and 1969), Texas (Simpson, 1954; Marwitz, 1986), Caribbean islands (Beebe, 1927; Breder, 1933), and Central America (Chacón et al., 1992).

Age and growth of tarpon are poorly documented. Previous age estimates based on the examination of scales suggest a maximum life span of about 15 years (Breder, 1944; de Menezes and Paiva, 1966). Studies on a variety of species show that scales are not reliable for ageing long-lived fishes and that scale-derived age estimates are typically lower than estimates derived from sectioned otoliths (Beamish and McFarlane, 1983; Casselman, 1983). Ageing of tarpon based on sectioned otoliths is needed to evaluate the accuracy of the ages estimated by Breder (1944) and de Menezes and Paiva (1966). In this article, we describe age and growth of tarpon from South Florida waters on the basis of an examination of sectioned otoliths.

## **Methods**

We obtained tarpon from a variety of sources throughout South Florida from April 1988 to November 1993. Most large fish (>1,100 mm FL) were obtained from taxidermists in Fort Myers and Fort Lauderdale; the fish had been caught in either the Florida Keys or Boca Grande Pass on Florida's Gulf coast (26°43'N, 82°16'W). A second source of large fish was tournaments held in the Keys, Boca Grande Pass, and the Tampa Bay area (27°40'N, 82°35'W). All large tarpon were caught with hook-and-line gear. Small tarpon (<1,100 mm FL) were taken with cast nets, hookand-line gear, electroshockers, trammel nets, and gill nets at various locations in South Florida. Young-ofthe-year tarpon were caught most effectively with cast nets of various mesh sizes and ranging in radius from 2.1 to 3.1 m. We sampled YOY tarpon monthly from November 1988 to April 1991 at two sites in South Florida. On the Atlantic coast, we sampled Jack Island State Park (27°30'N, 80°18'W),

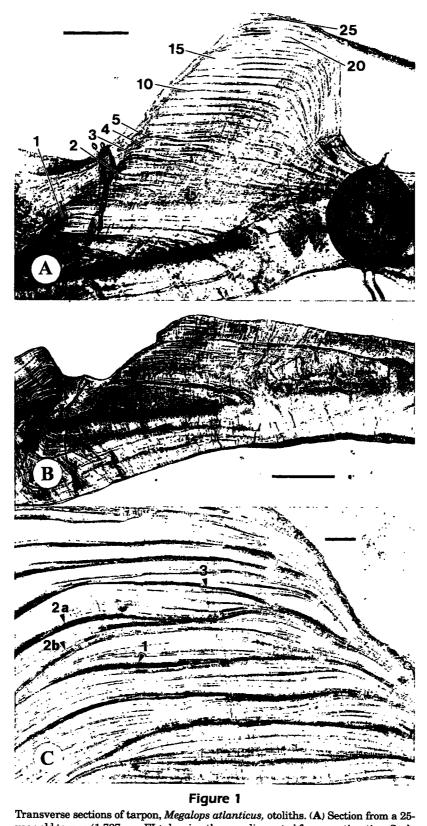
a 159.5-ha, impounded saltmarsh immediately adjacent to the Indian River Lagoon. The site consisted of a series of ditches that surrounded brackish wetlands and that were connected by flood gates to the Indian River Lagoon. The second site was located on the Gulf coast approximately 1.6 km south of U.S. Highway 41 and 3.2 km east of Collier-Seminole State Park near Naples (25°58'N, 81°33'W). This site consisted of a series of mangrove-lined ponds and borrow ditches resulting from road construction in the salt marsh.

Standard length (SL), fork length (FL), and total length (TL) were measured to the nearest millimeter (mm). All lengths reported are fork lengths. Large tarpon (>1,100 mm) were weighed to the nearest 0.5 kg, and smaller tarpon were weighed to the nearest gram. Otoliths (sagittae) were removed, cleaned with bleach (5.25% sodium hypochlorite), and rinsed first in water and then in 95% ethanol. Otoliths were stored dry or in 95% ethanol until sectioned. Sex was recorded and confirmed histologically.

Undamaged otoliths were weighed to the nearest 0.01 mg. Weights of left and right otoliths were not significantly different (paired t-test, n=270, t=0.039, P=0.97); therefore, otolith weights were pooled for analysis. If both left and right otolith weights were available for an individual fish, the mean of the two weights was calculated. Linear regressions were fit to  $\log_{10}$ -transformed otolith weight and age data and were compared with a t-test (Zar, 1984).

Generally, the left sagitta was used for age estimation; however, if the left otolith was broken, lost, or destroyed during processing, the right otolith was substituted. We prepared otoliths for age estimation by embedding them in Spurr (Secor et al., 1992), a high-density plastic medium. A 1-2 mm thick transverse section containing the otolith core was cut with a Beuhler Isomet low-speed saw with a diamond blade. The section was mounted on a microscope slide with thermoplastic glue (CrystalBond 509 adhesive) and polished with wet and dry sandpaper (grit sizes ranging from 220 to 2,000) until the annuli were visible. Sections were then polished on a Beuhler polishing cloth with 0.05-µ gamma alumina powder to remove scratches. Annuli were counted three times by each of two independent readers using compound microscopes. Mean counts of each reader were not significantly different (paired t-test, n=1,099, t=1.30, P=0.193); therefore, all six counts were used to calculate a mean age. All counts and measurements were made along the ventral sulcal ridge (Fig. 1A); the dorsal ridge was used only as an aid to interpretation. Measurements were made with an ocular micrometer.

Tarpon otoliths were often difficult to interpret; therefore, we established the following criteria to



Transverse sections of tarpon, *Megalops atlanticus*, otoliths. (A) Section from a 25-year-old tarpon (1,727 mm FL) showing the annuli counted for age estimation. Scale bar = 500  $\mu$ . (B) Section from a 2-year-old tarpon (506 mm FL) showing the notch formed on the edge of the sulcal ridge. Scale bar = 500  $\mu$ . (C) Section from a 33-year-old tarpon (1,615 mm FL) showing confluent annuli that were interpreted as a single annual mark. Marks 2a and 2b were counted as a single annulus. Scale bar = 50  $\mu$ .

provide a consistent basis for determining whether an annulus should be counted as an annual mark. For the 4–5 annual marks closest to the core, a notch was usually present on the ventral edge of the sulcal ridge (Fig. 1B). The notch was typically accompanied by an annulus extending outward to the otolith's ventral margin. If a distinct notch was present, the annulus was counted even if the mark extending outward was indistinct. Confluent annuli were counted as a single annual mark unless the two annuli were confluent for only a short distance (Fig. 1C). If many confluent marks were present, the otolith was rejected as unreadable.

Annulus counts for individual otoliths often showed some level of variation among readings. We established criteria for accepting or rejecting individual otoliths by calculating a coefficient of variation  $(CV) = (S/\overline{y} \times 100\%)$ , where S = the standard error of counts for a given otolith, and  $\overline{y}$  = the mean annulus count for a given otolith. CV precision criteria were calculated as  $CV = \sqrt{(n \times d^2)/t^2}$ , where n=the number of readings for a given otolith (6), d=the deviation allowed between the estimated mean increment count and the true count for a given otolith, and t=a one-tailed Student's t-statistic with  $\alpha = 0.05$ and n-1 degrees of freedom. We allowed a maximum deviation (d) of 10%, which corresponds to a CV of 12.16%. After six readings were completed, otoliths for which there were significant disagreements among readings (CV≥12.16%) were again examined by both readers in an attempt to reconcile differences. After discussing possible explanations for the variability among readings, a decision was made regarding the readability of the otolith. If both readers judged the otolith to be readable, it was again read independently by each reader without knowledge of the previous readings. The reading showing the largest difference from the mean of all readings was then discarded and replaced by a new reading. This protocol was repeated twice, and if the CV remained  $\geq 12.16\%$ , the otolith was rejected.

Tarpon typically spawn during May-August (Crabtree et al., 1992; Crabtree, 1995), and annulus formation took place during January-May. Consequently, annulus counts were not always equivalent to age in years. To resolve this discrepancy, fish collected before 1 July (the approximate middle of the spawning season) that had recently formed an annulus during the winter or spring (determined on the basis of the proximity of the annulus to the otolith's margin) were assigned an age one less than the annulus count. Fish collected after 1 July were assigned an age equal to the annulus count.

The von Bertalanffy (1957) growth equation  $FL_t = L_{\infty}(1 - e^{(-K(t-t_0))})$  was fit to observed age-length

data with the nonlinear regression procedure of Statgraphics. Likelihood-ratio tests were used to compare parameter estimates (Kimura, 1980; Cerrato, 1990). Length-weight regressions were calculated by linear regression of  $\log_{10}$ -transformed data and were compared with a t-test (Zar, 1984).

Tarpon were captured from the Sebastian River, located on Florida's Atlantic coast, by electroshocking or with trammel nets for age-validation experiments (Table 1). After capture, fish were sedated with MS-222, measured for fork length, and tagged with darttype tags. After tagging, tarpon were injected with Liquamycin LA-200 (200-mg oxytetracycline [OTC]/ mL) in the dorsal musculature at a dosage of 100mg OTC per kg fish weight. Fish weight was estimated with a length-weight equation. Tarpon were then transported to one of three holding facilities located in Florida, where they were held for 13 to 50 months (Table 1). Two fish were held in a 25-m by 13-m by 2.7-m deep public aguarium at Mote Marine Laboratory in Sarasota, six were held in a 33.5m by 5.5-m by 0.75-m deep pond at the Keys Marine Laboratory in Long Key, and 10 were held in a 9.1-m diameter by 2.0-m deep tank at the Florida Marine Research Institute's Stock Enhancement Research Facility (SERF) at Port Manatee. Fish were held at ambient temperatures in all facilities except in SERF, where heaters were used during the winter to prevent temperatures from dropping below 14°C. Tarpon were fed as much frozen fish as they would consume at least three times a week. Otolith sections were examined with a compound microscope (40-100×) equipped with ultraviolet light so that the fluorescent OTC marks could be detected.

## Results

The 1,469 tarpon we examined ranged from 102 to 2,045 mm in length; 740 (50.4%) of these were YOY or 1-year-old fish (<400 mm). Of these 740 small fish, we examined 179 histologically but could sex only 11 (6.1%); consequently, the sex of most YOY and 1-year-old tarpon was unknown and they were excluded from sex-specific regressions. Neither slopes (t-test, df=602, t=0.039, P=0.484) nor elevations (t-test, df=603, t=0.205, t=0.419) of the length-weight equations for male and female tarpon were significantly different. The pooled length-weight equation for sexed and unsexed fish and the relationships between SL, FL, and TL are presented in Table 2.

Female tarpon attained larger sizes than did males. Among the fish that we sexed, females ranged from 331 to 2,045 mm in length (median=1,635 mm, upper quartile=1,752 mm, n=412) and were signifi-

Table 1

Data for oxytetracycline (OTC)-injected tarpon, Megalops atlanticus. Otolith measurements were made along the ventral sulcal ridge from the otolith core to the OTC mark, annuli, and the otolith's edge. Measurements were made to the annulus at or just before the OTC mark and all subsequent annuli. Holding facilities are MOTE = Mote Marine Laboratory, KML = Keys Marine Laboratory, and SERF = Florida Marine Research Institute's Stock Enhancement and Research Facility.

Specimen number	Holding facility	Injected		Sacrificed					Distance from core (mm)					
		Date	Fork length (mm)	Date	Fork length (mm)	Months held	Age (years)	OTC mark	Annulus	Annulus	Annulus	Annulus	Annulus	Otolith edge
1137	MOTE	March 89	580	Oct 9	0 675	20	?	1.61	1.60					1.84
1138	MOTE	March 89	518	Oct 9	0 686	20	4	1.59	1.60	1.69				1.78
1486	KML	March 90	640	Sep 9	2 791	32	5	1.51	1.50	1.57	1.65			1.71
1487	KML	March 90	663	Sep 9	2 762	32	7	2.06	2.06	2.16	2.29			2.35
1488	KML	March 90		Sep 9	2 749	32	6	2.06	2.07	2.16	2.39			2.45
1489	KML	March 90	617	Sep 9	2 785	32	6	1.53	1.53	1.67	1.75			1.82
1490	KML	March 90	548	Sep 9	2 727	32	4	1.33	1.32	1.41	1.49			1.61
1568	KML	March 90		May 9	4 802	50	9	1.84	1.84	1.88	1.94	2.00	2.04	2.04
1548	SERF	Sep 92	570	Oct 9	3 762	13	?	1.67						1.80
1549	SERF	Sep 92		Oct 9	3 859	13	?	1.94						1.96
1559	SERF	Sep 92	890	May 9	4 1,005	21	?	2.25	2.25	2.35				2.37
15 <b>6</b> 0	SERF	Sep 92	670	May 9	4 805	21	7	1.84	1.81	1.86	1.98			1.98
1561	SERF	Sep 92		May 9	4 790	21	5	1.65	1.63	1.67	1.80			1.86
1562	SERF	Sep 92	750	May 9	4 900	21	8	2.04	2.04	2.16	2.24			2.25
1563	SERF	Sep 92	670	May 9	4 900	21	6	1.84	1.81	1.88	1.99			2.00
1564	SERF	Sep 92		May 9	4 805	21	4	1.53	1.44	1.55	1.76			1.78
1565	SERF	Sep 92	615	May 9	4 850	21	?	1.51						1.76
1566	SERF	Sep 92	760	May 9	4 950	21	?	1.80	1.82					1.86

cantly larger than males, which ranged from 203 to 1,884 mm in length (median=1,346 mm, upper quartile = 1,467 mm, n=203; Mann-Whitney U-test, P<0.001). The recreational harvest of tarpon in Florida consisted principally of large fish. Among the fish sampled from the recreational fishery, females ranged from 1,193 to 2,040 mm in length (mean = 1,677 mm, SD=141.5, n=322) and were significantly larger than males, which ranged from 901 to 1,884 mm in length (mean=1,447 mm, SD=130.2, n=125; t-test, t=15.77, t<0.001).

We examined OTC-marked otoliths from 18 tarpon (Table 1). Individuals showed increases in length ranging from 95 mm in 20 months to 235 mm in 21 months. Otoliths from 12 fish ranging in age from 4 to 9 years showed the expected pattern of otolith growth; one annulus had been formed per year. One tarpon (specimen number 1549) showed little otolith growth and formed no visible annuli while in captivity. Two tarpon (specimen numbers 1559 and 1566) that were sacrificed in May, 21 months after OTC injection, had lower annulus counts than expected. Otoliths from these two fish showed little growth

distally to the annulus during their first winter or spring in captivity. Otoliths from three other tarpon (specimen numbers 1137, 1548, and 1565) were problematic, and we were unable to estimate their ages. Annuli on these otoliths were indistinct, and we would have judged these otoliths to be unreadable had they come from wild fish. Five of the six fish whose otoliths were problematic were held in the heated facility at SERF and the other one was held at Mote Marine Laboratory. Otoliths from all six tarpon held in the flow-through facility at Keys Marine Laboratory had the expected pattern of one annulus per year.

Marginal-increment analysis of otoliths from YOY and 1-year-old tarpon suggested that one annulus formed each year. Young-of-the-year tarpon formed an annual mark sometime between December and May, and all YOY and 1-year-old tarpon otoliths had formed a first annulus by June (Fig. 2A). Mean marginal increments showed a seasonal minimum during April—June and a maximum in November (Fig. 2B). Marginal-increment analysis of older tarpon was not possible because of the incomplete seasonal coverage and limited sample sizes.

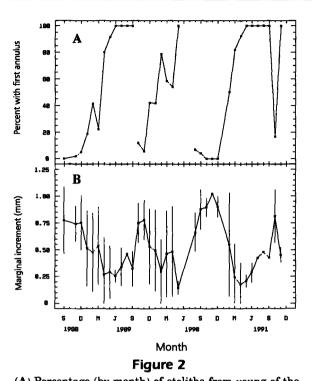
### Table 2

Length-length, length-weight, and otolith weight-age regressions for tarpon, *Megalops atlanticus*, from South Florida waters. TL = total length (mm), FL = fork length (mm), SL = standard length (mm), WT = weight (kg), OWT = otolith weight (g), and AGE= age in years. Sample fork-length range for all length-length regressions was 106–2,045 mm and for length-weight regressions was 102–2,045 mm; age range for the otolith weight-age regressions was 1–55 years for females and 1–43 years for males. Values in parentheses are standard errors.

		Y = a + bX						
Y	X	n	a	b	r <sup>2</sup>			
FL	SL	1,342	10.8404	1.0423	0.999			
			(0.6339)	(0.0007)				
FL	TL	1,061	-10.8096	0.8967	0.999			
		•	(0.8084)	(0.0007)				
SL	FL	1,342	-9.9770	0.9588	0.999			
		-	(0.6131)	(0.0007)				
SL	TL	1,051	-21.1779	0.8606	0.999			
			(1.0181)	(0.0009)				
TL	FL	1,061	12.6345	1.114	0.999			
			(0.8937)	(0.0009)				
TL	SL	1,051	25.5839	1.1607	0.999			
			(1.1622)	(0.0012)				
log <sub>10</sub> WT	$log_{10}FL$	1,262	-7.9156	2.9838	0.997			
			(0.0124)	(0.0045)				
log <sub>10</sub> OWT	$log_{10}AGE$	193	-1.2083	0.5476	0.872			
(females)	-9		(0.0199)	(0.0152)				
log <sub>10</sub> OWT	$log_{10}AGE$	106	-1.1734	0.4614	0.886			
(males)			(0.0183)	(0.0162)				

Of 1,231 otoliths processed for age estimation, 138 (11.2%) were judged unreadable by one or both readers and were not assigned ages, and an additional 116 (9.4%) otoliths were rejected for having high variation among readings (CV $\geq$ 12.16%); thus 977 (79.4%) otoliths were accepted for age estimates. Of these 977 otoliths, 470 (48.1%) were from YOY tarpon. The length-frequency distribution of fish whose otoliths were rejected because they were unsuitable for age estimation was not significantly different from that of all fish whose otoliths were examined ( $\chi^2$ =12.4, df=19, P=0.86).

Tarpon are long-lived; the oldest fish examined was a 2,045-mm female estimated to be 55 years old. The oldest male was 43 years old and had a length of 1,710 mm. Tarpon growth was rapid until an age of about 12 years, after which growth slowed considerably (Fig. 3). Likelihood-ratio tests showed a signifi-



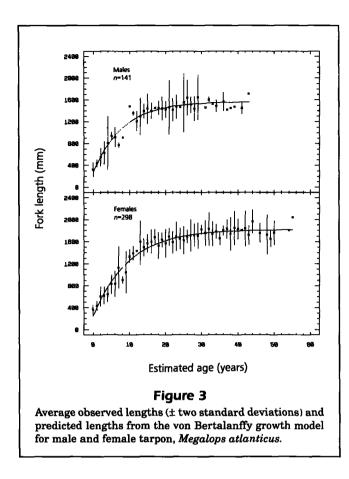
(A) Percentage (by month) of otoliths from young-of-theyear and 1-year-old tarpon, *Megalops atlanticus*, that had formed a first annulus. (B) Monthly mean marginal increment width and standard deviation for otoliths from youngof-the-year and 1-year-old tarpon.

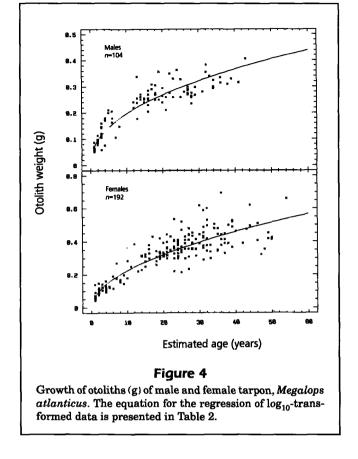
Table 3

Parameter estimates for the von Bertalanffy growth model for tarpon, *Megalops atlanticus*, collected in Florida. Values in parentheses are standard errors.

Sex	n	$L_{\omega}(\mathrm{mm})$	K	$t_{o}$	$r^2$
Males	141	1,566.6 (23.65)	0.123 (0.0090)	-1.575 (0.2519)	0.933
Females	298		0.103 (0.0049)	-1.410 (0.2158)	0.930

cant difference in the overall von Bertalanffy growth models for males and females ( $\chi^2=122.70$ , df=3, P<0.001, Table 3). Estimates of  $L_{\infty}$  ( $\chi^2=51.31$ , df=1, P<0.001) and  $K(\chi^2=4.48,$  df=1, P=0.036) also differed between the sexes, while  $t_0$  was not significantly different ( $\chi^2=0.28$ , df=1, P=0.58). Lengths at age predicted by the von Bertalanffy equation agreed with the average observed lengths of both female and male tarpon (Fig. 3). Predicted lengths at age of females were greater than those of males for all ages greater than 4 years (Table 4).





Otolith weight was significantly related to age (Fig. 4). The slopes of the otolith weight-age equations (Table 2) were significantly different for males and females (t-test, t=3.69, df=295, P<0.001).

## Discussion

We obtained tarpon from a variety of fishery-independent and fishery-dependent sources; consequently, our sample was biased towards certain size classes, and the size-frequency distribution of our sample may not reflect that of the population. Most small fish (<1,100 mm) came from fishery-independent sources, and larger fish were sampled from the recreational fishery. Our size distributions were bimodal and contained many small and large fish, but only a few fish 900–1,200 mm in length because these intermediate-size fish were too large to be sampled effectively by our gear and were rarely harvested in the recreational fishery. The size frequency of tarpon sampled from the recreational fishery was probably biased towards larger individuals. Most fish were caught during tournaments or were kept as trophies to be mounted by a taxidermist; presumably

in both situations anglers selectively kept larger fish. Sometimes tournaments imposed minimum size requirements of as much as 50 kg on the fish harvested. Because males were typically smaller than females and rarely exceeded 45 kg, our samples from the recreational fishery contained roughly twice as many females as males, but this probably does not reflect the population's sex ratio. Among the smaller tarpon (<1,100 mm) obtained from fishery-independent sources, there were 79 males and 85 females and the sex ratio was not significantly different from 1:1 ( $\gamma^2$ =0.230, df=1, P=0.064).

Age-validation experiments with OTC-marked otoliths supported the hypothesis that tarpon otoliths formed annual marks. Otoliths from 3 of the 18 OTC-injected tarpon showed fewer than the expected number of increments. These fish showed relatively little otolith growth following capture, and we were unable to resolve annuli that might have been present on the otolith's margin. We could not read the otoliths from three other tarpon and were unable to validate the periodicity of annulus formation for these fish. It is not surprising that several otoliths from OTC experiments were rejected as unreadable because almost 21% of otoliths from wild fish were unreadable;

**Table 4**Average observed and predicted fork lengths (mm) for male, female, and unsexed tarpon, *Megalops atlanticus*. Values in parentheses are standard error and sample size.

	Male	s	Femal	Unsexed	
Age (yr)	Average observed	Predicted	Average observed	Predicted	Average observed
0	321 (26.5;6)	276	362 (24.9;3)	246	239 (2.3;461)
1	440 (10.0;11)	425	434 (13.5;10)	400	396 (21.0;21)
2	552 (26.7;9)	557	607 (26.0;12)	538	547 (11.9:20)
3	626 (31.0;12)	674	621 (23.6;12)	664	626 (32.1;9)
4	806 (140.9;3)	777	645 (23.9;9)	777	
5	940 (20.8;3)	869	830 (36.6;6)	878	786 (154.0;2)
6	918 (45.4;4)	950	831 (58.7;4)	970	
7	774 (16.5;2)	1,021	1,130 (94.8;4)	1,053	
8	909 (1)	1,084	903 (22.5;2)	1,128	1,143 (1)
9		1,140	1,044 (95.3;4)	1,196	1,100(1)
LO	1,480 (1)	1,189	1,337 (41.5;2)	1,256	
1	1,359 (13.0;2)	1,233	1,391 (36.9;3)	1,311	921 (1)
<b>12</b>	1,205 (52.3;3)	1,272	1,435 (1)	1,361	1,310 (68.0;2)
13	1,295 (69.6;6)	1,306	1,601 (152.5;2)	1,406	
4	1,392 (29.7;5)	1,336	1,495 (39.6;4)	1,446	
15	1,435 (60.7;5)	1,363	1,568 (30.4;7)	1,482	1,385 (114.5;2)
L <b>6</b>	1,400 (26.9;7)	1,386	1,602 (38.2;8)	1,515	1,538 (1)
L <b>7</b>	1,451 (2.3;3)	1,407	1,684 (31.4;5)	1,545	1,317 (39.7;5)
l <b>8</b>	1,450 (23.0;8)	<b>1,426</b>	1,527 (39.2;9)	1,572	
19	1,443 (47.9;5)	1,442	1,633 (20.9;10)	1,596	
20	1,428 (42.8;3)	1,456	1,571 (49.1;7)	1,617	
21	1,465 (143.0;3)	1, <del>4</del> 69	1,691 (19.9;16)	1,637	
22	1,417 (61.3;3)	1,480	1,589 (41.8;6)	1,655	1,397 (1)
23	1,473 (76.0;2)	1,490	1,695 (37.7;12)	1,671	1,397 (1)
24	1,470 (5.0;2)	1,499	1,656 (23.1;17)	1,685	1,750(1)
25	1,550 (190.0;2)	1,507	1,625 (47.0;7)	1,698	1,498 (152.0;2
26	1,639 (114.5;2)	1,514	1,691 (24.1;6)	1,710	
27	1,513 (30.2;6)	1,520	1,710 (50.8;8)	1,720	
28	1,438 (55.7;4)	1,525	1,715 (34.6;9)	1,730	1,675 (1)
29	1,648 (119.2;3)	1,530	1,706 (38.5;9)	1,738	1,848 (120.5;2
30		1,534	1,818 (18.2;5)	1,746	
31	1,460 (1)	1,538	1,760 (29.7;15)	1,753	
32	1,604 (16.0;2)	1,541	1,824 (61.8;6)	1,759	
33	1,525 (1)	1,544	1,741 (38.6;8)	1,765	1,473 (1)
34	1,489 (32.8;3)	1,547	1,782 (37.6;3)	1,770	
35		1,549	1,658 (25.3;6)	1,775	
36	1,570 (60.0;2)	1,551	1,802 (19.2;5)	1,779	
37	1,422 (1)	1,553	1,830 (38.1;5)	1,783	
38	1,450 (1)	1,555	1,741 (85.0;3)	1,786	
39	1,473 (1)	1,556	1,846 (77.0;4)	1,789	
10	1 440 480 0 0	1,557	1,827 (52.4;3)	1,792	
1	1,448 (38.0;2)	1,558	1,800 (1)	1,795	1 500 (1)
2	1.710/**	1,559	1,835 (115.0;2)	1,797	1,580 (1)
13	1,710(1)	1,560	1,718 (49.5;3)	1,799	
4			1,965 (75.0;2)	1,801	
5			4 888 (50.00)	1,802	
6			1,755 (50.3;3)	1,804	
.7			4 808 (405 0.0)	1,805	4 000 (00 0 0 0
8			1,727 (127.0;2)	1,806	1,679 (73.0;2)
19			1,656 (44.1;3)	1,808	
50			1,762 (63.2;3)	1,809	
51				1,809	
52				1,810	
53				1,811	
54			1,800 (1)	1,812	
55			2,045 (1)	1,812	

thus, we expected at least this percentage of otoliths from captive fish to be unreadable. Indeed, it is likely that captive conditions and nonseasonal food availability diminished the seasonal nature of otolith growth in captive fish and thereby increased the difficulties in otolith interpretation. Our use of heaters at SERF during the winter reduced the seasonal change in water temperature; five of the six fish with problematic otoliths were held at this facility. We used the heaters at SERF during winter cold fronts when water temperatures might have reached low levels lethal to tarpon. Otoliths from all six of the tarpon held in the flow-through facility at Keys Marine Laboratory, where water at ambient temperature was continuously pumped from Florida Bay, showed the expected pattern of one annulus formed per year.

Marginal-increment analyses also supported our hypothesis that the marks we counted formed once per year. The consistent marginal-increment minima observed for YOY and 1-year-old tarpon suggest that the marks present on otoliths of these fish were annual marks formed during winter or spring.

Additional support for the validity of our age estimates comes from the life span of a captive tarpon placed in the John G. Shedd Aquarium in Chicago, Illinois, in November 1935. This tarpon was still alive in April 1994 and was at least 59 years old confirming that tarpon can reach ages of more than 50 years as our data suggest.

Tarpon otoliths had annuli on both the dorsal and ventral sulcal ridges that were similar in appearance to validated annuli in other species. Typically, annuli on the ventral ridge were more easily distinguished, and annulus counts from this ridge were usually higher than annulus counts from the dorsal ridge. Some otoliths had regions where bands were distorted, unclear, or confluent, making counts difficult or impossible. In other otoliths, portions of the sulcal ridge were dark in color and annuli were obscured. Our rejection of many otoliths as unreadable could have biased our growth-parameter estimates, but the size distribution of tarpon with otoliths judged to be unreadable was not significantly different from that of all tarpon examined for age and growth. Thus, we did not systematically reject a higher proportion of larger and presumably older fish than smaller and presumably younger tarpon. We do not know if rejected otoliths tended to come from faster- or slower-growing tarpon; this is a potential source of bias in our growth-parameter estimates.

We could not sex most of the 0-, 1-, and 2-year-old tarpon examined and this is another potential source

of bias in our growth models. Observed lengths at age for the males and females we could sex at ages 0–2 were larger than the observed lengths of unsexed fish (Table 4). It is likely that the 0-, 1-, and 2-year-old fish we could sex were precocious and thus larger than comparably aged fish that we could not sex. Consequently, our sex-specific growth models were biased towards larger fish at these young ages; however, the predicted lengths at age from both sex-specific growth models at ages 0, 1, and 2 were between the observed lengths of sexed and unsexed fish, thus this bias was probably small. In addition, because both growth models included over 40 year classes, this bias probably had little effect on our growth-parameter estimates.

Tarpon scales do not appear to be suitable for age estimation. Scale-derived estimates of tarpon longevity by Breder (1944) and de Menezes and Paiva (1966) suggested a maximum age of only 15 years, much lower than our otolith-derived estimate of 55 years and the known age of captive tarpon. De Menezes and Paiva (1966) presented scale-derived estimates of von Bertalanffy growth parameters for tarpon and estimated that for males,  $L_{m}=2,062$  mm, K=0.084, and  $t_0$ =0.20 and for females,  $L_{\infty}$ =2,633, K=0.065, and  $t_0 = 0.17$ . These estimates are probably biased by a consistent underestimation of ages and are considerably different from our otolith-derived estimates. Scale-derived estimates of  $L_{\infty}$  are unrealistically high and are much larger than the maximum size documented for any tarpon.

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## Literature cited

## Beamish, R. J., and G. A. McFarlane.

1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735-743.

#### Beebe, W.

1927. A tarpon nursery in Haiti. Bull. N.Y. Zool. Soc. 30:141-145.

#### Breder, C. M.

1933. Young tarpon on Andros Island. Bull. N.Y. Zool. Soc. 36:65-67.

1944. Materials for the study of the life history of Tarpon atlanticus. Zoologica 29:217-252.

## Casselman, J. M.

1983. Age and growth assessment of fish from their calcified structures—techniques and tools. In E. D. Prince and L. M. Pulos (eds.), Proceedings of the international workshop on age determination of oceanic pelagic fishes: tunas, billfishes, and sharks, p. 1–17. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 8.

## Cerrato, R. M.

1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Can. J. Fish. Aquat. Sci. 47:1416-1426.

## Chacón Chaverri, D., and W. O. McLarney.

1992. Desarrollo temprano del sábalo, Megalops atlanticus (Pisces: Megalopidae). Rev. Biol. Trop. 40:171-177.

## Crabtree, R. E.

1995. Relationship between lunar phase and spawning activity of tarpon, *Megalops atlanticus*, with notes on the distribution of larvae. Bull. Mar. Sci. 56:895-899.

# Crabtree, R. E., E. C. Cyr, R. E. Bishop, L. M. Falkenstein, and J. M. Dean.

1992. Age and growth of tarpon, Megalops atlanticus, larvae in the eastern Gulf of Mexico, with notes on relative abundance and probable spawning areas. Environ. Biol. Fish. 35:361-370.

## de Menezes, M. F., and M. P. Paiva.

1966. Notes on the biology of tarpon, *Tarpon atlanticus* (Cuvier and Valenciennes), from coastal waters of Ceara State, Brazil. Arg. Estac. Biol. Mar. Univ. Fed. Ceara 6:83-98.

## Erdman, D. S.

1960. Larvae of tarpon, Megalops atlantica, from the Anasco River, Puerto Rico. Copeia 1960:146.

## Harrington, R. W.

1958. Morphometry and ecology of small tarpon, Megalops atlantica Valenciennes, from transitional stage through onset of scale formation. Copeia 1958:1-10.

1966. Changes through one year in the growth rates of tarpon, *Megalops atlanticus*, Valenciennes, reared from mid-metamorphosis. Bull. Mar. Sci. 16:863-883.

#### Hildebrand, S. F.

1934. The capture of a young tarpon, Tarpon atlanticus, at Beaufort, North Carolina. Copeia 1934:45-46.

1963. Family Elopidae. In H. B. Bigelow (ed.), Fishes of the western North Atlantic. Mem. Sears Found. Mar. Res. Yale Univ. 1(3):111-131.

#### Kimura, D. K.

1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77:765-776.

### Marwitz, S. R.

1986. Young tarpon in a roadside ditch near Matagorda Bay in Calhoun County, TX. Texas Parks Wildl. Dep., Coastal Fish. Branch, Manage. Data Ser. No. 100, 8 p.

#### Mercado, J. E., and A. Ciardelli.

1972. Contribución a la morfología y organogénesis de los leptocéfalos del sábalo Megalops atlanticus (Pisces: Megalopidae). Bull. Mar. Sci. 22:153-184.

#### Rickards, W. L.

1968. Ecology and growth of juvenile tarpon, *Megalops atlanticus*, in a Georgia salt marsh. Bull. Mar. Sci. 18:220-239.

#### Secor, D. H., J. M. Dean, and E. H. Laban.

1992. Otolith removal and preparation for microstructural examination. In D. K. Stevenson and S. E. Campana (eds.), Otolith microstructure examination and analysis, p. 19-57. Can. Spec. Publ. Fish. Aquat. Sci. 117.

## Simpson, D. G.

1954. Two small tarpon from Texas. Copeia 1954:71-72. Smith, D. G.

1980. Early larvae of the tarpon, Megalops atlantica Valenciennes (Pisces: Elopidae), with notes on spawning in the Gulf of Mexico and the Yucatan Channel. Bull. Mar. Sci. 30:136-141.

## Tucker, J. W., and R. G. Hodson.

1976. Early and mid-metamorphic larvae of the tarpon, Megalops atlanticus, from the Cape Fear River estuary, North Carolina, 1973-1974. Chesapeake Sci. 17:123-125.

## von Bertalanffy, L.

1957. Quantitative laws in metabolism and growth. Q. Rev. Biol. 32:217-231.

## Wade, R. A.

1962. The biology of the tarpon, Megalops atlanticus, and the ox-eye, Megalops cyprinoides, with emphasis on larval development. Bull. Mar. Sci. 12:545-603.

1969. Ecology of juvenile tarpon and effects of dieldrin on two associated species. Tech. Pap. Bur. Sport Fish. Wildl. 41:1-85.

## Zale, A. V., and S. G. Merrifield.

1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Florida)—ladyfish and tarpon. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.104). U.S. Army Corps Eng. TR EL-82-4, 17 p.

## Zar, J. H.

1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, NJ, 718 p.